VOLUME XII NUMBER 2

MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

Contents

April, 1953

MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

Re-entered as second-class matter February 19, 1952, at the post office at Lincoln, Nebraska, under the act of March 3, 1879.

Established 1916. Published quarterly. Subscription price $4.00 per year. Completed volumes I to VIII, $5.00 each; volume IX, $6.00; volume X, $7.00; Volume XI, $8.00; single numbers, see back cover.

Published at 440 South 11th Street, Lincoln, Nebraska

for the

CALIFORNIA BOTANICAL SOCIETY, INC.

Annual membership dues of the California Botanical Society are $4.00, which includes a year's subscription to Madroño. For two members of the same family the dues are $5.00, which includes one copy of Madroño, and all other privileges for both. Dues should be remitted to the Treasurer. General correspondence, changes of address, and applications for membership should be addressed to the Secretary.

NEW SPECIES AND CHANGES IN NOMENCLATURE IN THE GENUS CLARKIA (ONAGRACEAE)

Harlan Lewis and Margaret Lewis

The genus *Clarkia* has recently been the subject of extensive morphological and cytogenetical studies which indicate that *Clarkia, Godetia, Phaeostoma,* and *Eucharidium* form a natural interrelated group that should be treated taxonomically as a single genus. This is not a new idea. *Clarkia, Phaeostoma* and *Eucharidium* have been considered congeneric by most recent authors (e.g., Munz & Hitchcock, 1929; Jepson, 1936). Nelson and Macbride (1916) suggested that *Godetia* should be combined with *Clarkia* because they could find no consistent differentiating characters. They subsequently (1918) made most of the appropriate transfers. More recently Hiorth (1941) has examined the morphological characters that have been used to differentiate *Clarkia* and *Godetia* and has concluded that the entire group can be treated reasonably only as a single genus, but he did not adopt the generic name *Clarkia* for the species with which he worked.

We are now preparing a monograph of *Clarkia* which will present a detailed account of the relationships within the genus. In the meantime it seems desirable to publish formally certain new species and combinations in order that they may be used for other discussions.

Type specimens, permanent slides, and herbarium vouchers of collections for which chromosome numbers are given are on file at the University of California, Los Angeles.

Changes in Nomenclature

Clarkia bottae comb. nov. *Godetia bottae* Spach, Nouv. Ann. Mus. Par. 4:393. 1835.

Clarkia cyclindrica comb. nov. *Godetia bottae* var. *cylindrica* Jepson, Univ. Calif. Publ. Bot. 2:332. 1907.

Clarkia davyi comb. nov. *Godetia quadrivulnera* var. *Davyi* Jepson, *op. cit.* p. 341.

Clarkia deflexa comb. nov. *Godetia deflexa* Jepson, *op. cit.* p. 332.

Clarkia gracilis (Piper) Nels. & Macbr. subsp. **albicaulis** comb. nov. *Godetia amoena* var. *albicaulis* Jepson, *op. cit.* p. 329.

Clarkia gracilis (Piper) Nels. & Macbr. subsp. **sonomensis** comb. nov. *Godetia amoena* var. *sonomensis* Hitchcock, Bot. Gaz. 89:338. 1930.

Clarkia lassenensis comb. nov. *Godetia lassenensis* Eastwood, Leafl. West. Bot. 2:281. 1940.

Madroño, Vol. 12, No. 1, pp. 1–32. February 4, 1953.

Clarkia mildrediae comb. nov. *Phaeostoma mildredae* Heller, Leafl. West. Bot. 2:221. 1940.

Clarkia rubicunda comb. nov. *Godetia rubicunda* Lindley, Bot. Reg. t. 1856. 1836.

Clarkia speciosa nom. nov. *Godetia parviflora* (H. & A.) Jepson, *op. cit.* p. 339, based upon the type of *Oenothera viminea* var. *parviflora* H. & A. Bot. Beech. Voy. 342. 1840. Not *Clarkia parviflora* Eastwood, Bull. Torrey Bot. Club 30:492. 1903.

Clarkia tenella comb. nov. *Oenothera tenella* Cav. Ic. 4:66, t. 396. 1797.

Clarkia williamsonii comb. nov. *Godetia williamsoni* Durand & Hilgard, Pac. R. Rep. 5 (3) : 7, t. 5. 1855.

New Species

Clarkia affinis sp. nov. Herba erecta altitudine ad 8 dm.; caulibus simplicibus vel superne ramosis; foliis linearibus vel angusto-lanceolatis, integris, 1.5–7 cm. longis, 2–3 mm. latis; inflorescentium axe erecto; calycis tubo 1.5–4 mm. longo et annulo pilorum ad medium vel infra, posito, limbo 5–10 (14) mm. longo, 1.5–2 mm. lato sub anthesi connato et declinato; petalis obovatis 5–15 mm. longis pallido-roseis vel roseo-purpureis et frequens ad basim pallidioribus purpureo-punctulatis; staminibus 8, plerumque stigmate adhaerentibus; stigmate quadrifido, lobis brevibus; stylo stamina aequante; ovario gracile cinereo-pubescente 1.2–5 cm. longo, 8-canaliculato; capsula 1.5–3 cm. longa, 2 mm. lata.

An erect herb, as much as 8 dm. tall, simple or branched above; stems slender, puberulent above with short upwardly curled hairs, sparsely puberulent or glabrate below; leaves linear to narrowly lanceolate, entire, puberulent, 1.5–7 cm. long, 2–5 mm. broad, sessile or narrowed into petioles as much as 3 mm. long; rachis of the inflorescence erect; buds erect; hypanthium obconical, puberulent with appressed hairs, 1.5–4 mm. long, the ring of hairs at or below the middle; sepals lanceolate, often attenuate at the tip, 5–10 (rarely 14) mm. long, 1.5–2 mm. broad, appressed puberulent, usually remaining united and deflexed to one side in anthesis; petals obovate, subentire to erose, 5–15 mm. long, pale pink to lavender-pink, sometimes dark reddish-purple, usually lighter near the base, often flecked or pencilled with purple; stamens 8, in two series, white to yellow, sometimes purple spotted, usually adhering to the stigma and depositing the cream or whitish pollen upon it as the flower opens; stigma lavender to purple with 4 short lobes; style shorter than the stamens; ovary slender, densely gray puberulent with short upwardly appressed hairs, 1–2.5 cm. long, shallowly 8-grooved, sessile or sometimes on pedicels as much as 4 mm. long, gradually tapering into a short beak; capsules 1.5–3 cm. long, about 2 mm. broad, straight or slightly curved.

Type. Santa Margarita to Pozo road, 9.8 miles east of the junction with the road to Creston, San Luis Obispo County, California, May 2, 1947, *Lewis and Epling 181.*

The haploid chromosome number is 26. The populations that have been determined include the type collection.

Clarkia affinis (n = 26) is an allohexaploid species closely related to *C. purpurea* (Curtis) Nels. and Macbr. (n = 26). Cytological examination of the hybrid between them indicates that they probably have a tetraploid parent (n = 17) in common, but that they each have a different diploid (n = 9) parent. *Clarkia affinis* and *C. purpurea* apparently hybridize occasionally in nature (Mt. Diablo) and the F1 hybrid produces a few seeds when open pollinated in the garden. The petals of *C. affinis* are often flecked; the sepals remain united and turned to one side at anthesis and the capsule is slender. The petals of *C. purpurea,* on the other hand, are not flecked; the sepals are individually reflexed at anthesis and the capsule is stocky.

Distribution. California: South Coast Ranges from Ventura County to Santa Clara, Alameda, and Contra Costa counties, and north of San Francisco Bay in Lake, Napa, Solano, and Yolo counties.

Representative specimens. Alameda County: Corral Hollow road 18.0 miles west of junction with U.S. Highway 50 at Tracy, *Lewis & Epling 198;* lower part of Arroyo Mocho, *Howell 18104.* Contra Costa County: 3.7 miles ENE of Tassajero, *Belshaw 2114;* north side of Mt. Diablo, *Howell 6483.* Monterey County: Pleyto road 2.0 miles south of the Bradley-Jolon road, *Lewis & Epling 193;* 2.5 miles north-northwest of Pleyto Well, *Graham 400.* San Benito County: 5 miles from Panoche—Idria road near mouth of canyon of Griswold Creek, *Wiggins & Ferris 9368;* 6 miles east of Paicines, *Howell 12969, 12970.* San Luis Obispo County: 8.8 miles west of U.S. Highway 101 on the northern road to Adelaida, *Lewis & Epling 189;* roadside 2 miles east of Santa Margarita on State Highway 178, *Ferris & Rossback 9432.* Santa Barbara County: summit of Nojoqui Pass, Santa Ynez Mts., *Keck & Hiesey 5138.* Santa Clara County: near Cupertino, *Heller 8552;* Uvas-Almaden road, *Mason 6947.* Solano County: near Vacaville, *Jepson* in 1891. Ventura County: Ojai Valley, *Hall 3192.* Yolo County: banks of Putah Creek near Winters, *Heller & Brown 5584.*

Clarkia lingulata sp. nov. Herba erecta altitudine ad 6 dm.; foliis lineari-lanceolatis, denticulatis, 2–6 cm. longis, 2–8 mm. latis, basi in petiolos etiam 1.5 cm. longos angustatis; inflorescentium axe apice recurvato; calycis tubo 1–4 mm. longo, annulo pilorum ad apicem posito, limbo 7–10 mm. longo, 1–1.5 mm. lato, roseo-purpureo, sub anthesi connato et declinato; petalis lingulatis vel oblanceolatis pallido-rubris, 1–2 cm. longis, 5–8 mm. latis; staminibus 8, quam stylus brevioribus; stigmate

quadrifido, lobis brevibus; ovario 8-costato; capsula quadrangula 1–2 cm. longa, 1.5 mm. lata.

Erect, as much as 6 dm. tall; stems simple or branched above, puberulent above with short upwardly curled hairs, sparsely puberulent below; leaf blades linear to narrowly lanceolate, denticulate to entire, 2–6 cm. long, 2–8 mm. broad, glabrate to sparsely puberulent, narrowed into petioles as much as 1.5 cm. long; rachis of the inflorescence recurved in bud, becoming erect as the flowers open, the buds pendulous; hypanthium 1–4 mm. long, the ring of hairs in the upper third; sepals lanceolate, 7–10 mm. long, 1–1.5 mm. broad, bright pink or purplish, remaining united and deflexed to one side at anthesis; petals oblanceolate, obtuse, entire or minutely notched at the summit, 1–2 cm. long, 5–8 mm. broad, bright pink, sometimes flecked with red; stamens 8, in two series, the outer blue with blue pollen, the inner shorter, white to cream with white to cream pollen; stigma white to reddish-purple with 4 short lobes; mature style exceeding the stamens, pinkish; ovary conspicuously 8-ribbed, puberulent, becoming bright green and shining, 5–10 mm. long, sessile or on pedicels as much as 7 mm. long; mature capsules straight or nearly so, quadrangular, 1–2 cm. long, about 1.5 mm. broad.

Type. Merced River 0.2 mile west of bridge over South Fork, Mariposa County, California, June 8, 1947, *Lewis & Lewis 334.*

The haploid chromosome number is 9. Samples from both of the known populations, including the type collection, have been determined.

Clarkia lingulata (n = 9) is most closely related to *C. biloba* (Dur.) Nels. & Macbr. (n = 8), from which it differs morphologically in the shape of the petal. These two species form essentially sterile hybrids when crossed in the garden.

Distribution. Known from only two localities on State Highway 140 along the Merced River, Mariposa County, California—0.2 mile west of bridge over South Fork (the type locality), *Lewis & Lewis 334; 625; Lewis, Lewis & Roberts 698, 801;* between 7.4 and 7.5 miles east of Bear Creek Bridge, *Lewis & Lewis 629, Lewis, Lewis & Roberts 703, 796, 797.*

Clarkia prostrata sp. nov. Herba prostrata vel decumbens; caulibus etiam 5 dm. longis, simplicibus vel ramosis et divaricatis; foliis oblanceolatis vel elliptis, plerumque obtusis, 1–2.5 cm. longis, 4–8 mm. latis, sessilibus; inflorescentium axe recto; calycis tubo 4–7 mm. longo, annulo pilorum infra medium posito, limbo 6–10 mm. longo, 2–3 mm. lato sub anthesi per paria recurvato; petalis obovatis interdum truncatis, 10–15 mm. longis, roseo-purpureis basi pallidioribus vel luteolis plerumque rubro-maculatis; staminibus 8; stylo stamina plus minusve aequante; stigmate quadrifido, lobis brevibus; capsula 8-costata, 2–3 cm. longa, 2.5–3 mm. lata.

Prostrate or decumbent, the stems as much as 5 dm. long, simple or divaricately branched, sparsely puberulent above with short upwardly curled hairs, sparsely puberulent to glabrate below; leaf blades oblanceolate to elliptic, 1–2.5 cm. long, 4–8 mm. broad, entire or nearly so, the apex usually obtuse, glabrate to sparsely puberulent, sessile or nearly so; rachis of the inflorescence straight, buds erect; hypanthium 4–7 mm. long, sometimes rosy on the outside, the ring of hairs in the lower third; sepals lanceolate, 6–8 mm. long, 2–3 mm. broad, puberulent, usually reflexed in pairs; petals fan-shaped to truncate-obovate, entire to erose or emarginate, 10–15 mm. long, lavender-pink shading to cream or pale yellow below, usually with a deltoid blotch of bright reddish-purple at the base of the lavender-pink; stamens 8; anthers cream; pollen cream; stigma 4–lobed, the lobes short; mature style equalling the shorter stamens; ovary puberulent, 10–18 mm. long, strongly 8-ribbed, sessile or essentially so; mature capsules straight to somewhat curved, quadrangular, 2–3 cm. long, 2.5–3 mm. broad.

Type. State Highway 1, 1.3 miles north of Pico Creek bridge, between San Simeon and Cambria, San Luis Obispo County, California, June 10, 1950, *Lewis & Lewis 712.*

The haploid chromosome number is 26. The type collection has not been counted. The material examined cytologically was from seeds collected near Piedras Blancas Point, San Luis Obispo County, by Dr. R. F. Hoover (our accession number *169).*

Clarkia prostrata ($n = 26$) is an allohexaploid species of the sea bluffs in San Luis Obispo and Monterey counties, and morphologically closely resembles *C. davyi* (Jepson) Lewis & Lewis ($n = 17$), a tetraploid species of the sea bluffs of San Mateo to Humboldt counties. It differs from *C. davyi* in having larger flowers and a reddish blotch of color in the middle or lower part of the petal.

Distribution. California: sea bluffs of San Luis Obispo and Monterey counties and Santa Rosa Island, Santa Barbara County.

Specimens examined. Monterey County: Monterey, *Abbott* in 1904, *Guirado 638;* Pacific Grove, *Patterson & Wiltz* in 1907. San Luis Obispo County: State Highway 1, 0.5 miles south of Carpojo Bridge, *Lewis & Lewis 714;* Piedras Blancas, *Eastwood & Howell 5983;* State Highway 1, 0.5 miles north of Piedras Blancas, *Lewis & Lewis 713;* 1 mile north of mouth of Pico Creek (2.5 miles southeast of San Simeon), *Keck & Hiesey 5150;* San Simeon Bay near Cambria, *Eastwood 15148;* between Cambria and San Simeon, *Eastwood & Howell 5973;* Cambria, *Winblad* in 1937, *Eastwood & Howell 5943, Lewis & Lewis 711;* Morro Bay, *Condit* in 1911. Santa Barbara County: Santa Rosa Island, Water Canyon, *Hoffman 692;* Santa Rosa Island, *Dunn* in 1932, *Youngberg* in 1938, *Hoffman* in 1930.

Clarkia imbricata sp. nov. Herba erecta altitudine ad 6 dm., foliis crebris, imbricatis, ascendentibus, lanceolatis, 2–2.5 cm. longis, 4–7 mm. latis, integris vel denticulatis, sessilibus vel a petiolis ad 2 mm. longis extenuatis; inflorescentis densis; calycis tubo 1–1.5 cm. longo, infundibuliformi, ad 10 mm. lato, annulo pilorum infra medium ornato, limbo 1–1.5 cm. longo, 3–5 mm. lato, sub anthesi per paria recurvato; petalis flabelliformibus 2–2.5 cm. longis, roseo-purpureis apice purpureis cuneato-maculatisque; staminibus 8, quam stylus brevioribus; stigmate quadrifido, lobis 2 mm. longis purpureis; capsula immatura 8-costata, 1–1.5 cm. longa, 4–5 mm. lata, ea matura 3 mm. lata.

An erect herb, as much as 6 dm. tall, unbranched or with numerous short branches in the upper parts, sometimes with a few large branches from the base, densely leafy; leaves lanceolate, 2–2.5 cm. long, 4–7 mm. broad, entire to denticulate, ascending, overlapping, longer than the internodes, sessile or on petioles less than 2 mm. long; inflorescence congested; flowers showy; hypanthium conspicuous, 1–1.5 cm. long, funnelform, flaring above the ring of hairs, as much as 1 cm. broad, conspicuously veined, the ring of hairs about 3 mm. above the base; sepals lanceolate, 1–1.5 cm. long, 3–5 mm. broad, remaining united in pairs or reflexed individually; petals fan-shaped, 2–2.5 cm. long, lavender above, pale lavender to nearly white below, light purple at the base; with a conspicuous V-shaped purple spot which extends from the middle to the upper margin of the petals; stamens 8, in two similar series, lavender, the filaments of the outer series about twice the length of the inner; pollen white; stigma lobes 2 mm. long, dark purple, held above the stamens; immature capsule 1–1.5 cm. long, 4–5 mm. broad, conspicuously and deeply 8-ribbed; mature capsule ribbed, 3 mm. broad, the beak short, less than 1 mm. long.

Type. Roadside at 6230 Vine Hill Road between Santa Rosa and Guerneville, adjacent to Pitkin Ranch, Sonoma County, California, July 10, 1951, *Lewis & Lewis 865*.

The haploid chromosome number is 8, determined from material from the type collection.

Clarkia imbricata is morphologically similar to *C. williamsonii* ($n = 9$), *C. speciosa* ($n = 9$), and certain races of *C. purpurea* ($n = 26$). It can be distinguished from them by the broad, overlapping, ascending leaves.

Distribution. Known only from the type and the following collections, all from one small area in Sonoma County, California. Pitkin Ranch along path to marsh, *M. S. Baker 11017*; dry slope bordering Pitkin Marsh, *Howell 12315*.

Acknowledgements

Herbarium material has been kindly loaned to us from the California Academy of Sciences, Dudley Herbarium of Stanford University, Pomona College, University of California at

Berkeley, Washington State College, Rocky Mountain Herbarium, Philadelphia Academy of Sciences, Missouri Botanical Garden, United States National Herbarium, New York Botanical Garden, and Gray Herbarium. We are greatly indebted to the curators of these herbaria. We are also indebted to Prof. Carl Epling for assistance with the Latin diagnoses. Many of the chromosome determinations were made while the senior author was a National Research Council Fellow in residence at the John Innes Horticultural Institution, Merton (now at Bayfordbury) England.

Department of Botany,
University of California, Los Angeles.

LITERATURE CITED

HIORTH, G. 1941. Zur Genetik und Systematik der Gattung Godetia. Zeit. f. Ind. Abst—u. Vererb, 79: 199–219.
HITCHCOCK, C. L. 1930. Revision of North American species of Godetia. Bot. Gaz. 89: 321–361.
JEPSON, W. L. 1936. Flora of California 2: 573–586.
MUNZ, P. A. & C. L. HITCHCOCK. 1929. A study of the genus Clarkia, with special reference to its relationship to Godetia. Bull. Torrey Bot. Club 56: 181–197.
NELSON, A. & J. F. MACBRIDE. 1916. Western plant studies III. Bot. Gaz. 61: 30–47.
NELSON, A. &. J. F. MACBRIDE. 1918. Western plant studies V. Bot. Gaz. 65: 58–70.

RELICT ISLANDS OF XERIC FLORA WEST OF THE CASCADE MOUNTAINS IN OREGON

LEROY E. DETLING

A student of the Pacific Northwest flora frequently has his attention called to the occasional occurrence west of the Cascade crest of plant species whose normal range is in the more arid regions of the Rogue River Basin to the southward, or the basins and plateaus east of the Cascades. Closer investigation reveals some rather significant features in the distribution of some of these outliers—features which may have a bearing upon the study of the origins and past migrations of the Northwest flora.

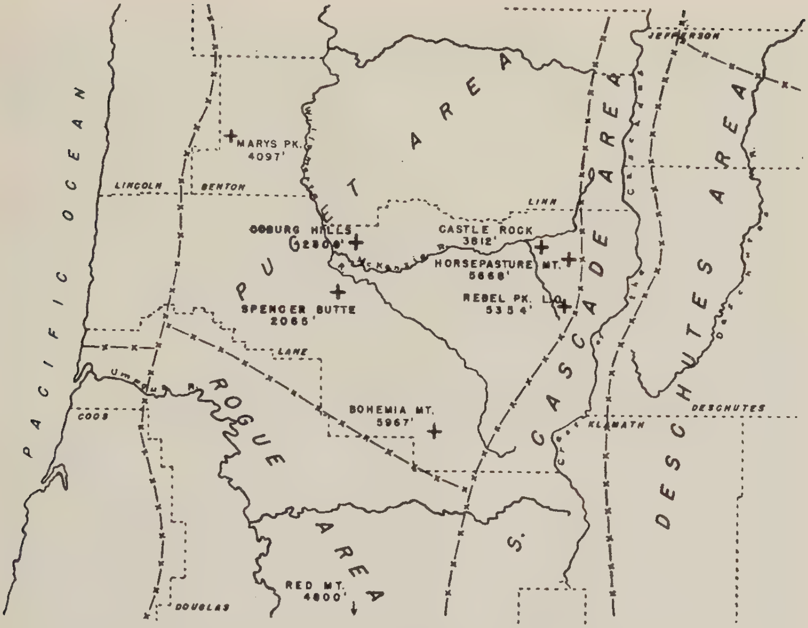
In the first place, the stations where any one of the species is found are not scattered indiscriminately over the region west of the mountains. On the contrary, they are relatively few in number and in each station several to many of the outlier species are concentrated within a restricted area. In the second place, these restricted areas are in all cases mountain summits where a special set of environmental conditions obtains, producing a habitat differing considerably from that immediately surrounding it, and similar in many respects to those found

in the Rogue River Valley or the regions east of the Cascades. In other words, these summits constitute isolated "islands" of xeric flora within a general mesic region.

The writer has made a study of eight of these islands (see accompanying map and table of xeric species), and the results and conclusions are presented herewith. Field studies, which have included all these islands, have been supplemented by herbarium study at the University of Oregon and Oregon State College. Collections made by Rayma Brown on Spencer Butte, Roy Andrews on Horsepasture Mountain, and J. Rollo Patterson and Wm. H. Baker (1951) in the Bohemia-Fairview district were of great value.

With one exception all these islands are located along the west slopes of the Cascade Mountains in Lane and Douglas counties, Oregon. The exception, Marys Peak, is in the heart of the Oregon Coast Range in Benton County. All but Red Mountain are included in that vegetation area which we have designated as the Puget (to be explained in a later paragraph). The latter is in the northern part of the Rogue Area. The general region is one of moderate to excessive annual precipitation, most of which falls during the winter, and of moderate summer and winter temperatures. Elevations of the peaks range from about 2000 feet on Spencer Butte, near Eugene, to nearly 6000 feet in the Bohemia-Fairview district. The most easterly of the islands is the one on Horsepasture Mountain, which is about twenty miles in a straight line from the nearest ponderosa pine forests of eastern Oregon. These twenty miles, however, include the unbroken belt of subalpine vegetation along the crest of the Cascades.

In each case the peak is composed of a mass of igneous rock which has been eroded away to form an isolated point or short ridge. As erosion has progressed, the soil originating from the rock at the summit has largely been washed down the slope, leaving a mass of rock either completely exposed or covered over with a thin layer of soil. There is no indication that the surrounding forest trees or deep-rooted shrubs have ever been able to invade these places. The shallow soil is subject to rapid drainage, and the vegetation is exposed to the dessicating action of sun and wind. Temperatures are undoubtedly affected by heat absorption by the dark rocks and by the protection afforded by crevices and rock ledges. One significant effect of this would probably be the lengthening of the growing season for those plants established in this situation. It is under these conditions of moisture and temperature and without serious competition with the surrounding species that we find the xeric flora which we are discussing. The mountain slopes below the islands are in all instances covered with moderately dense forest. Below 4500 feet this forest is made up of Douglas fir (*Pseudotsuga taxifolia*) with its associated



vine maple (*Acer circinatum*), Oregon grape (*Berberis nervosa*), and salal (*Gaultheria Shallon*). Above this elevation it is mixed with, or even replaced by, such types as noble fir (*Abies procera*), subalpine fir (*A. lasiocarpa*), western white pine (*Pinus monticola*), and mountain hemlock (*Tsuga Mertensiana*). For the sake of comparison it is of interest to note that as yet no xeric species have been found to occur on the summit of Hardesty Mountain, a peak within this area which reaches an elevation of 4250 feet. In this case, for some reason, a moderately deep soil cover has been retained at the summit, allowing a dense growth of *Pseudotsuga, Castanopsis,* and *Rhododendron* to become established there.

From the results of several seasons' collecting on the eight floral islands we have selected thirty-two species whose normal distribution is in the more arid vegetation areas to the south or east. Undoubtedly the list would be extended by more thorough collecting on the same peaks as well as by the inclusion of other peaks of similar environmental conditions in the same general region. The accompanying table indicates the occurrence of the species on the islands under consideration. Considerable variation is apparent in the number occurring in any one island. Of particular interest is Rebel Peak, in the watershed of the South Fork of the McKenzie River, where no less than eighteen xeric species are either directly associated with, or among rocks in the immediate vicinity of a patch of *Arte-*

misia tridentata, the only occurrence of this sagebrush known to the writer from west of the Cascade Mountains.

The isolated character of the several islands gives evidence of their being relicts of a former widespread xeric flora. It is generally conceded by students of plant distribution that such islands are left in favorable niches in the wake of retreating or shrinking populations. An advancing population, on the other hand, presents a relatively continuous front, and is not preceded to any great distance by outliers of its species.

The chief significance of our xeric islands lies in their relation to the floras of the four or five vegetation areas which are in closest proximity to them, and particularly to the three among this number in which the relict species have their normal range today. For the purpose of this discussion these areas will be referred to by the names adopted by the writer in a previous study (Detling, 1948). The first is the Rogue Area, comprising roughly the valleys of the Rogue and Umpqua rivers. The second area, the Deschutes, includes the plateau and basin region east of the Cascades and south of the Ochoco and Blue Mountains, extending to Klamath and Summer lakes, and to the northeastern corner of Nevada. The Columbia Area takes in, in a general way, the valleys of the middle Columbia River and its main tributaries in north central Oregon and south central Washington. The Puget Area is made up of the valleys of the Willamette-Puget Trough, and extends from the Rogue Area northward to southwestern British Columbia. Finally, the higher elevations of the Cascade Mountains between the Columbia and Klamath rivers comprise the South Cascade Area.

The xeric flora alluded to was presumably at one time the basic flora of the Puget Area, including the west slopes of the Cascades up to an elevation of nearly 6000 feet, probably the highest altitude at which the relicts now occur. Since the relicts in their normal range are largely associates of the ponderosa pine forests, we must assume that at the time the xeric flora occupied the Puget Area the latter had a climate comparable to that which now obtains in the Rogue, Deschutes, and Columbia areas, where continuous stands of this pine are now extant. Annual precipitation would have ranged from twelve to forty-five inches (less than half that of the present period); January mean temperatures must have ranged between 26° F. and 40° F., while July mean temperatures were probably from 60° F. to 73° F. Evidence of such a warm-dry cycle in the Pacific Northwest, culminating about six to eight thousand years ago, is offered by the bog-pollen studies of Hansen (1947). According to these studies the warm, dry climate probably persisted in this area until as late as about four thousand years ago. It seems quite possible, therefore, that a xeric flora such as is today associated with the ponderosa pines was the dominant

feature of the west slopes of the Cascades as recently as that. Hansen (op. cit.) finds no evidence of any increase of this species in the Willamette Valley during the post-glacial dry period, and he suggests the possibility that the scattered stands now found in the southern end of the valley may be the result of a more recent invasion. In any case, it is difficult to explain the absence of ponderosa pine today above the level of the valley floor in the Puget Area other than by supposing that competition with other forest types has eliminated it completely from the deeper soils, while at the same time, due to its deep-rooted habit, it has never been able to persist on the rocky, shallow soils of the mountain summits and ridges.

Returning to the present distribution of the plant species in the relict islands, we find that each falls into one of six distinct patterns. These patterns may be summarized in the following manner, each group of species having its normal distribution in the area or areas indicated in the appropriate heading:

I. Rogue. *Erigeron foliosus confinis, Hieracium cynoglossoides nudicaule, Sidalcea asprella, Viola Sheltonii.*

II. Deschutes. *Arenaria formosa, Bromus polyanthus, Lupinus lepidus medius.*

III. Rogue-Deschutes. *Collomia linearis, Delphinium depauperatum, Eriogonum umbellatum, Madia minima.*

IV. Rogue-Columbia. *Eriogonum compositum pilicaule, Sisyrinchium Douglasii.*

V. Rogue-Deschutes-Columbia. *Arabis Holboellii retrofracta, Claytonia lanceolata, Crocidium multicaule, Erythronium grandiflorum pallidum, Gilia aggregata, Hackelia diffusa, Linum Lewisii, Lupinus laxiflorus, Microsteris humilis, Phacelia linearis, Poa scabrella, Prunus emarginata, Sanicula graveolens, Sedum Douglasii.*

VI. Deschutes-Columbia. *Arnica Parryi, Artemisia tridentata, Polygonum Douglasii, Silene Douglasii.*

None of the thirty-two species under consideration has its normal distribution in the Columbia Area alone.

In a previous paper (Detling, op. cit.) the writer has emphasized the point that the important feature of any vegetation area is not its boundaries, which are vague under the best of conditions, but rather its "environmental center," the point about which are grouped the extremes of environmental factors which produce the optimum conditions for the plant species inhabiting the area. Since in the last analysis the positions of these environmental centers are determined by the physiography of a region, it is highly probable that they have been relatively fixed for many thousands of years. If the climate of the Pacific Northwest were to shift toward a warm-dry maximum, the environmental extremes in such areas as the Rogue and Deschutes would become intensified, their influence would

spread progressively from the center outward, and their floras would advance at the expense of those areas, like the South Cascade, with a cool-moist combination of extremes. The reverse movement would occur as the climate became again cooler and more humid.

The South Cascade Area, with its marked extremes of moisture and low temperatures is interposed between the Deschutes and Puget areas in such a way as to hinder if not actually prevent any interchange of floral elements between these two until what was probably the culmination of a warm-dry cycle. Minimum elevations of the Cascade crest in this region are approximately 5000 feet, with most of the ridges rising at least 1000 or 1500 feet above this. A xeric Puget flora would have reached the elevation of all but the very highest of what are now the relict islands before contact would be made with a similar xeric flora east of the crest.

No such intervening area is interposed between the Rogue and the Puget, and the boundary separating the two is relatively indefinite. With a general increase in dryness and warmth, it is reasonable to suppose that a xeric flora advancing from the Rogue would reach the west slopes of the central Oregon Cascades before a similar xeric flora would cross the crest of the range from the Deschutes, and therefore that a large part of this element as it occurs in the Puget Area migrated in from the south.

What appears to be strong evidence in support of this theory is the distribution of those species in groups I and IV above, comprising about 18 per cent of the total xeric flora. These are Rogue species which are either restricted to that area except for the outliers in the Puget islands, or have an additional center of distribution in the Columbia Area, but in either case are absent from the Deschutes. A striking example of the latter type of distribution is that of *Eriogonum compositum*. The typical variety of this species with glabrous stems and peduncles is found commonly east of the Cascades except in a portion of the Columbia Area. The variety *pilicaule*, with pubescent stems and peduncles, replaces this in the Rogue and in the Columbia Area just eastward of the Columbia Gorge, and is the only form found on the Puget islands, where it occurs with considerable frequency.

A somewhat similar distribution pattern is presented by Garry oak (*Quercus Garryana*). This species extends northward from the central valley of California through the valleys of the Rogue and Puget areas to Vancouver Island and the lower Fraser River. An arm of its range extends through the Columbia River Gorge and eastward along the middle Columbia River and its tributaries. So far, it has not been reported as occurring east of the Cascades between the lower Deschutes River Valley and the Klamath River. In the Puget Area it is

largely restricted to the drier, lower elevations of the broad valleys, although it does occur on two or three of the xeric islands.

Several other species have this same distribution, e.g., *Dentaria tenella* var. *pulcherrima,* which is very abundant in the Rogue River Valley, fairly common in Hood River, Wasco, and Klickitat counties, and is found at rare stations in the Puget Area, including the Bohemia-Fairview island.

While this *Quercus* and *Dentaria* type of distribution does involve parts of the Puget Area other than the islands, and consequently ought perhaps to be considered as a special case, nevertheless it is of interest in this discussion in that it does emphasize the close relationship between the Rogue and Columbia areas, and the fact that this relationship does not necessarily involve the Deschutes Area at all.

An interesting species whose distribution pattern does not coincide with any of those cited above is *Allium crenulatum.* It occurs on three of our xeric islands, on Saddle Mountain in Clatsop County, Oregon, and in the Olympic Mountains of western Washington. According to Dr. Marion Ownbey (unpublished correspondence), its closest affinity seems to be with *A. parvum,* a species occurring east of the Cascades, and is part of a complex of xeric species having its center of dispersal to the south of our area.

While it seems reasonable that the earlier immigrants of the ponderosa pine flora reached the Puget Area from the south, when the upper limits of this flora reached the level of the Cascade crest under the influence of the extreme dryness and warmth, there probably was an influx of additional species from the east. This may have been the pathway of many of those relicts whose present normal distribution does not include the Rogue Area. Whether any of these species were ever present in the Rogue is problematical. The floras of the Rogue River Valley and the Klamath Basin have a great many species in common today, and there is no reason to doubt that at one time there may have been more of these, which have since disappeared from one or the other of the areas.

Where the various elements of the xeric flora came from in the first place is not within the scope of the present paper. Those which did not originate in the massif of the Siskiyou Mountains seem to have reached its eastern valleys and plateaus from the lower slopes of the Sierra Nevada or the central valley of California. From this point some of the species apparently continued northward on the east side of the Cascades, while others migrated westward to the valleys and canyons of the Siskiyou Mountains and thence to the Rogue River, possibly by way of the gap north of the Shasta Valley. Why they may have taken these divergent pathways is a subject for future investigation.

TABLE 1. DISTRIBUTION OF XERIC SPECIES AMONG THE RELICT ISLANDS

Xeric species	Red Mountain	Bohemia-Fairview	Rebel Peak Lookout	Horsepasture Mountain	Castle Rock	Spencer Butte	Coburg Hills	Marys Peak
Allium crenulatum		x					x	x
Arabis Holboellii retrofracta	x							
Arenaria formosa		x	x					
Arnica Parryi			x	x				
Artemisia tridentata			x					
Bromus polyanthus		x	x					
Claytonia lanceolata		x						
Collomia linearis			x					
Crocidium multicaule						x	x	
Delphinium depauperatum	x	x						
Erigeron foliosus confinis		x			x			
Eriogonum compositum pilicaule		x	x	x	x			
Eriogonum umbellatum		x	x	x				x
Erythronium grandiflorum pallidum	x	x						x
Gilia aggregata		x	x	x				
Hackelia diffusa			x					
Hieracium cynoglossoides nudicaule		x						
Linum Lewisii		x	x					
Lupinus laxiflorus			x	x		x	x	
Lupinus lepidus medius		x						
Madia minima					x			
Microsteris humilis		x	x					
Phacelia linearis						x	x	
Poa scabrella						x	x	
Polygonum Douglasii		x	x	x		x		
Prunus emarginata		x	x					
Sanicula graveolens		x	x	x				
Sedum Douglasii		x	x	x		x		
Sidalcea asprella							x	
Silene Douglasii			x	x				x
Sisyrinchium Douglasii						x		
Viola Sheltonii		x				x	x	

SUMMARY

Distribution patterns of thirty-two xeric plant species occurring on isolated mountain tops west of the Cascade Mountains of Oregon suggest that they are relicts of a once widespread xeric flora which originated, first, in the Rogue River Valley, and secondly, on the plateaus of east-central Oregon.

They have persisted on the mountain summits because of the arid and relatively warm conditions of the shallow soil and exposed dark rocks, and the consequent freedom from competition with the surrounding mesic forest types.

Museum of Natural History
University of Oregon, Eugene

Literature Cited

Baker, W. H. 1951. Plants of Fairview Mountain, Calapooya Range, Oregon. Am. Mid. Nat. 46: 132–173.

Detling, L. E. 1948. Concentration of environmental extremes as the basis for vegetation areas. Madroño 9: 169–185.

Hansen, H. P. 1947. Postglacial forest succession, climate, and chronology in the Pacific Northwest. Trans. Am. Philos. Soc. 37: 1–130.

Fig. 1. Location of islands of xeric flora in central western Oregon.

BALSAMORHIZA TEREBINTHACEA AND OTHER HYBRID BALSAM-ROOTS

William A. Weber

Balsamorhiza terebinthacea (Hook.) Nutt. was one of the earliest described taxa in the genus *Balsamorhiza.* It first appeared in the literature as *Heliopsis* (?) *terebinthacea* Hooker ([1834] 1840) and was described in the same article with the type species, *Balsamorhiza Hookeri,* which Hooker called *Heliopsis* (?) *balsamorhiza.* The taxon has been accepted as a species by most subsequent authors, including Peck (1941), Rydberg (1917), St. John (1937), and by the monographer of the genus, Ward M. Sharp (1935).

Hooker's diagnosis was as follows (the italics by the present author):

> H.? terebinthacea: pubescens, foliis radicalibus *petiolatis–ovato-lanceolatis sinuato–pinnatifidis crenato–serratis,* involucri foliolis numerosis lanceolato–acuminatis imbricatis caulem paucifoliatum subaequantibus, radice crassa balsamifera. Hab. Common at Fort Vancouver, on the Columbia, and in the grounds of the interior. Douglas.—*Closely allied to the preceding species* [H. balsamorhiza], and yielding in its root the same terebinthine juice.

In studies on natural hybridization in the genus *Balsamorhiza,* Ownbey and Weber (1943) showed that intersectional crosses between species of the Section *Eubalsamorhiza,* with pinnatifid leaves, and the Section *Artorhiza,* with triangular-cordate leaves, result in introgressants which tend to preserve the habit and leaf-size of the *Artorhiza* parent while they pick up various degrees of the lobing of the *Eubalsamorhiza* parent. Thus, a large number of intermediate individuals occur which have the general leaf outline of the *Artorhiza* species, but which possess leaf-margins varying from a few scattered crenate teeth all the way to deeply and irregularly pinnatifid. In taxonomic practice, these individuals have been called *Balsamorhiza terebinthacea.*

The type specimen of *B. terebinthacea* (fig. 1) is such an individual. It is apparently a derivative of the cross, *B. deltoidea* Nutt. × *B. Hookeri* (Hook.) Nutt., since this is the only combination of parental types which occurs in the vicinity of the type locality. In addition to the type specimen, Sharp (1935), in his monograph of the genus, cited the following specimens under his treatment of *B. terebinthacea* which probably represent hybrids of other parental combinations: *Suksdorf 10866, 360, 135,* Klickitat County, Washington, = *B. Careyana* × *B. Hookeri; Peck 8456,* Josephine County, Oregon, = *B. deltoidea* × *B. platylepis; Butler 1337,* Siskiyou County, California = *B. deltoidea* × *B. Hookeri* var. *lanata.* Similar individuals occur throughout the Pacific Northwest wherever the ranges and habitats of *Artorhiza* and *Eubalsamorhiza* species overlap.

It can be demonstrated, therefore, that *Balsamorhiza terebinthacea* is not a natural taxon except as it represents similar phenotypes obtained from crosses involving different pairs of species. It has, nevertheless, been a convenient name under which to file intermediate specimens in the herbarium when only one specimen from a given population is available. Unfortunately, collectors often seek out the unusual form in a population and neglect to preserve the typical specimens of the parental types which might indicate the probable parentage.

Although the name *B. terebinthacea* has provided a convenient category for filing the progeny of *B. deltoidea* and *B. Hookeri* crosses, as well as intermediate forms of unknown parentage, the writer feels it best not to encumber nomenclature by giving names to all hybrids of various parental combinations. The better course would be to designate as hybrids those names that have already been published as species, and in the future, whenever possible, refer to other known hybrids by their parental names connected by an ×. Previously published names in *Balsamorhiza* that can now be designated as hybrids, and their parental equivalents, are cited below.

× **Balsamorhiza terebinthacea** (Hook.) Nutt. Trans. Am. Philos. Soc. II. 7:349. 1841, hybrid, *B. deltoidea* Nutt. × *B. Hookeri* (Hook.) Nutt.

× **Balsamorhiza Bonseri** St. John, Fl. S.E. Wash. and Adj. Idaho, 1937, hybrid, *B. rosea* Nels. & Macbride × *B. sagittata* (Pursh) Nutt.

× **Balsamorhiza tomentosa** Rydberg, Bull. Torrey Club 27: 628. 1900 (*B. incana* var. *tomentosa* Sharp), hybrid, *B. incana* Nutt. × *B. sagittata* (Pursh) Nutt.

University of Colorado
Boulder, Colorado

References Cited

Hooker, W. J. [1834] 1940. Flora Boreali-Americana. London, H. G. Bohn.

PLATE 1. TYPE SPECIMEN OF BALSAMORHIZA TEREBINTHACEA (HOOK.) NUTT.

Ownbey, Marion, and William A. Weber. 1943. Natural hybridization in the genus *Balsamorhiza*. Am. Jour. Bot. 30: 179–187.
Peck, Morton E. 1941. A manual of the higher plants of Oregon. Binfords & Mort, Portland, Oregon.
Rydberg, Per Axel. 1917. Flora of the Rocky Mountains and adjacent plains. Published by the author.
Sharp, Ward M. 1935. A critical study of certain epappose genera of the Heliantheae-Verbesininae of the natural family Compositae. Ann. Mo. Bot. Gard. 22: 51–152.
St. John, Harold. 1937. Flora of Southeastern Washington and adjacent Idaho. Students Book Corporation, Pullman, Washington.

Plate 1. Type Specimen of Balsamorhiza terebinthacea (Hook.) Nutt.

THE RELATIONSHIP BETWEEN QUERCUS DUMOSA AND QUERCUS TURBINELLA

John M. Tucker

Quercus turbinella Greene and *Q. dumosa* Nutt. are closely related oaks; both commonly occur as chaparral shrubs, and both have small, hard, evergreen leaves which are very similar in shape. Although similar in these respects, in their most distinctive states they exhibit a number of differences—morphological, ecological, and geographical. Their ranges overlap in southern California, however, and in this area they intergrade to a greater or lesser degree. The purpose of this paper is to record the results of a study of this intergradation. The author's opinions regarding their taxonomic treatment are presented elsewhere (Tucker, 1952).

Differences between Quercus dumosa and Q. turbinella

The range of *Q. dumosa* and that of the typical subspecies of *Q. turbinella* are evidently completely disjunct. The latter occurs in California only in the New York Mountains of eastern San Bernardino County, ranging eastward to western Texas and recurring in northern Baja California (the type locality). *Quercus dumosa* does not occur as far east as the New York Mountains, and in Baja California it is apparently isolated from *Q. turbinella*.

The Californian subspecies (*Q. turbinella* subsp. *californica* Tucker) does, however, overlap the range of *Q. dumosa*, although ecologically they are in large part separated from one another. *Quercus turbinella californica* is the scrub oak component of the pinyon pine-juniper association of arid mountain slopes near or bordering the western edge of the Mohave Desert, and also occurs in the more arid parts of the inner South Coast Ranges. *Quercus dumosa* is a common element of the slightly more mesic chaparral of semi-arid, interior mountain slopes of southern California (although its range extends northward as far as Tehama County). Where these

associations meet in interior southern California, the two oaks tend to intergrade.

In gross aspect *Q. dumosa* and *Q. turbinella* subsp. *californica* are quite similar in several respects. In their most distinctive states, however, they differ in a number of morphological characteristics, as follows:

TABLE 1. MORPHOLOGICAL DIFFERENCES BETWEEN QUERCUS TURBINELLA CALIFORNICA AND Q. DUMOSA.

Q. turbinella californica	*Q. dumosa*
1. Upper leaf surface gray to gray-green; dull, not shining	1. Upper leaf surface green and shining
2. Leaf margin spinose-dentate (teeth with definite short spines to 1 mm. long)	2. Leaf margin usually mucronate-dentate to entire or subspinose; only infrequently definitely spinose
3. Twigs of the current season densely yellow-gray tomentose	3. Twigs of the current season pubescent to glabrate and brownish
4. Acorn cups thin	4. Acorn cups thick
5. Cup scales scarcely (or not at all) tuberculate	5. Cup scales (especially basal ones) usually strongly tuberculate
6. Cups turbinate to subhemipheric (or deeply cup-shaped) but the margins not turning inward	6. Cups hemispheric to about ⅔ spherical, the margins tapering inward

They tend to differ also in the size and shape of their buds and the shape of their acorns. In *Q. turbinella* the mature terminal buds are commonly small (1–2 mm. long) and globose, where as in *Q. dumosa* they are larger and usually ovoid. Acorns of the former are relatively slender and taper gradually to the pointed apex; those of the latter are broader in proportion to their length, and roundish at the apex.

Classification of these oaks has varied considerably with different authors. Some have regarded them as two distinct species; others have treated *Q. turbinella* as a variety of *Q. dumosa* (the older name); and still others have considered *Q. turbinella* to be merely a form of *Q. dumosa* unworthy of even varietal status (for a more detailed discussion of their taxonomic history see Tucker, op. cit.). As evidenced by their morphological similarity, it has been generally acknowledged that a close relationship exists between them. Their intergradation, however, has probably been the major factor causing some authors to treat them as elements of a single species.

Thanks are due the curators of the following herbaria for the loan of specimens: Pomona College (POM); San Diego Society of Natural History Herbarium (SD); University of

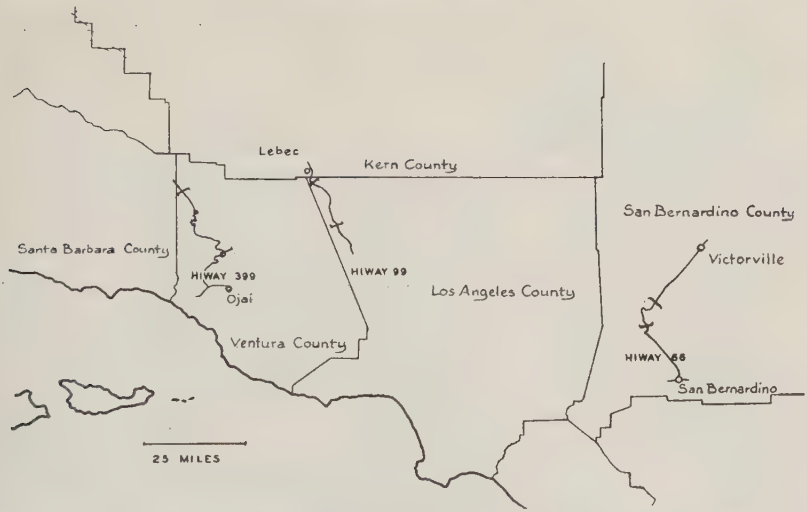


FIG. 1. Location of transects across zone of intergradation between *Quercus turbinella* and *Q. dumosa* in southern California.

California, Berkeley (UC); and University of California, Los Angeles (LA). Specimens in the writer's personal collection are cited by his initials (JMT).

POPULATION SAMPLES

In order to obtain more pertinent and detailed data than was possible from the study of miscellaneous herbarium specimens alone, three series of population samples ("mass collections"; cf. Anderson, 1941) were collected in southern California along transects across the zone of intergradation (fig. 1). The series along Highway 399 over Pine Mountain in northwestern Ventura County was collected on February 16, 1946, by Dr. G. L. Stebbins, Jr., Dr. C. H. Muller, and Mr. Clifton Smith. The other two were collected by the author with the help of his wife—one on October 18 and 19, 1946, along the Ridge Route (Highway 99) in northwestern Los Angeles County, the other on October 20, 1946, along Highway 66 over Cajon Pass in southwestern San Bernardino County. The location and the number of individuals in each population sample are given in Table 2.

For the analysis of these collections a hybrid index (cf. Anderson, 1936; Goodwin, 1937; Heiser, 1947; and Stebbins et al, 1947) was constructed on the basis of the six differences between *Q. turbinella californica* and *Q. dumosa* listed in Table 1. Since these differences were not all of the same degree or constancy, the characters were not all assigned the same index values. In each case the minimum value is characteristic of *Q. turbinella*, and the maximum is characteristic of *Q. dumosa*. During this analysis, "standard" specimens of *Q. dumosa, Q.*

TABLE 2. POPULATION SAMPLES OF QUERCUS DUMOSA AND Q. TURBINELLA SSP. CALIFORNICA.

Collection number	No. of individuals in sample	Location
		Pine Mountain Transect, Ventura County (fig. 2).
3607[1]	20	upper Cayama Valley, 6.6 mi. north of Lockwood Valley Rd.
3608	23	north base of Pine Mountain, .3 mi. south of Lockwood Valley Rd.
3609	20	north slope of Pine Mountain, 3 mi. south of Lockwood Valley Rd.
3610	17	north side of Pine Mountain, .5 mi. north of summit
3614	18	along Sespe Creek, 17.4 mi. north of Wheeler's Hot Springs
3615	21	along Sespe Creek, 15.7 mi. north of Wheeler's Hot Springs
3616	28	along Sespe Creek, 14.2 mi. north of Wheeler's Hot Springs
3617	20	summit of grade between Wheeler's Hot Springs and Sespe Creek
		Ridge Route Transect, Los Angeles County (fig. 3).
1467	27	ca. 3 mi. south of Lebec, Kern Co.
1477	18	18 mi. north of Castaic
1478	30	16.9 mi. north of Castaic
1479	29	16.3 mi. north of Castaic
1480	21	16.1 mi. north of Castaic
1481	30	15.8 mi. north of Castaic
1482	21	at top of ridge, 6.4 mi. north of Castaic
		Cajon Pass Transect, San Bernardino County (fig. 4).
1483	25	7.1 mi. northeast of junction with Highway 138
1484	25	4.8 mi. northeast of junction with Highway 138
1485	20	1.9 mi. southeast of junction with Highway 138

[1]Collection numbers in the Pine Mountain Transect are those of G. L. Stebbins, Jr.; in the Ridge Route and Cajon Pass transects they are those of the author.

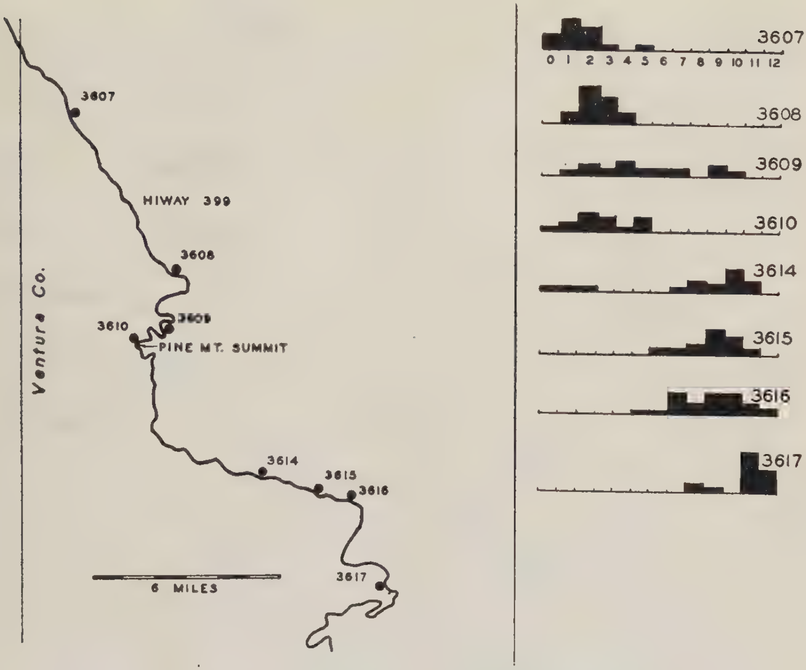


FIG. 2. Pine Mountain Transect, Ventura County.

turbinella californica, and intermediates were kept at hand for comparison. Each individual was scored on the six characters, the sum of these scores representing an index total for that particular plant. The totals for each population sample are presented in the form of a histogram.

Ratings on the six differences were as follows:

1. *Leaf color*. This is the most sharply distinct difference; hence a wider range between extremes of index scores, 0 to 4, was allowed than on any of the others.

2. *Leaf margin*. Three categories were recognized, scoring 0 to 2.

3. *Twig pubescence*. Since, in either oak, this is somewhat more variable than the other characters, only two categories were recognized, scoring 0 and 1.

4. *Thickness of acorn cup*. Three categories were recognized, scoring 0 to 2.

5. *Cup scales*. Three categories were recognized, scoring 0 to 2.

6. *Cup shape*. Since these oaks are not sharply separated on this difference, only two conditions were recognized, scoring 0 and 1.

Results and Discussion

In the histograms in figs. 2, 3, and 4, index totals are shown by the horizontal scale, and the number of plants is indicated

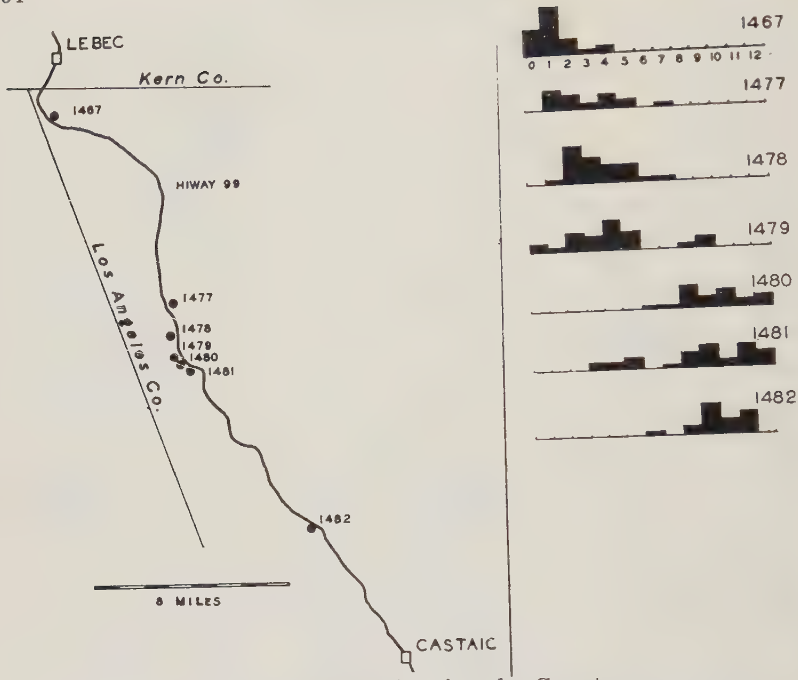


FIG. 3. Ridge Route Transect, Los Angeles County.

by the heights of the vertical columns. For the sake of discussion and comparison, individuals whose totals fall in the five lowest classes (0–4 inclusive) will be considered "good" *Q. turbinella,* since characters of this species received low scores. The "purest" collection of the latter made in this study, *Tucker 1467,* exhibits this range of index totals (fig. 3). Those whose totals fall in the five highest classes (8–12 inclusive) will be considered "good" *Q. dumosa,* since characters of this species received high scores. The "purest" collection, *Stebbins 3617,* exhibits this range (fig. 2). The remaining classes, of course, comprise the intermediate range.

In analyzing certain of these population samples, it seemed that cup characters often varied widely within the sample, while leaf characters were more consistent. To determine the degree of correlation between foliage and cup characters, therefore, a series of scatter diagrams was plotted (fig. 5). For each individual the total score on cup characters was plotted (as the ordinate) against the total on leaf and twig characters (as the abscissa).

PINE MOUNTAIN TRANSECT (figs. 2 and 5A). It is evident that *Stebbins 3607* is a collection of essentially "good" *Q. turbinella,* and, conversely, that *Stebbins 3617* is a collection of "good" *Q. dumosa.* Plotted on the same base line, they would present a discontinuous distribution, which indicates that, as they

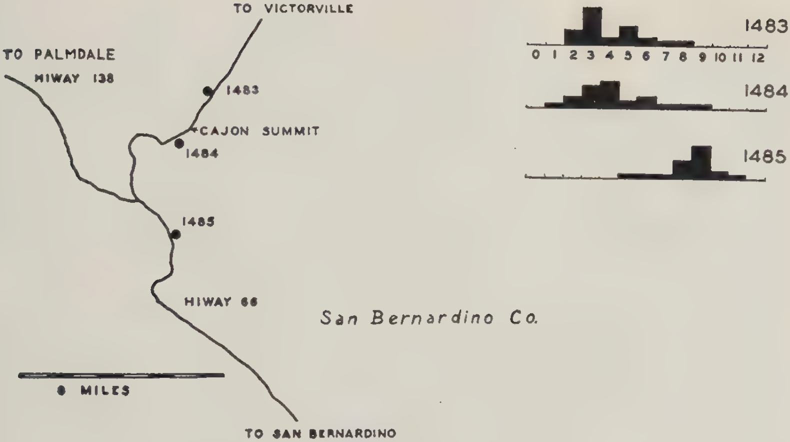


FIG. 4. Cajon Pass Transect, San Bernardino County.

occur in their respective habitats, they are morphologically quite distinct in the aggregate of characters scored.

Most of the other collections have a larger proportion in the intermediate range. Indeed, in *Stebbins 3609* the intermediates form a nearly continuous series between *Q. turbinella* and *Q. dumosa*. On the other hand, in *Stebbins 3614*, which also includes individuals of both species, there is only one *Q. dumosa*-like individual in the intermediate range.

These data indicate that in an occasional population along this transect the morphological gap between *Q. turbinella* and *Q. dumosa* may be bridged by intermediates, but this is not always the case. Any given population usually is composed mainly of one entity or the other, together with some intermediates. The presence of these intermediates suggests that populations of *Q. turbinella* and *Q. dumosa* have been reciprocally modified through introgression.

The scatter diagrams (fig. 5A) for this transect reveal one interesting point. In the collections that are predominantly *Q. dumosa* on the basis of index totals (*Stebbins 3614–3617*), the total scores on cup characters alone are distinctly more variable than the totals on leaf and twig characters. In *Stebbins 3616*, for example, all the leaf and twig totals lie in the higher (*Q. dumosa*) half of the range; the cup totals, however, are spread over the entire range. On the other hand, the collections that are predominantly *Q. turbinella* (*Stebbins 3607–3610*) do not show any conspicuous difference in variability between cup totals and leaf and twig totals. A tentative explanation is given following discussion of the other two transects.

RIDGE ROUTE TRANSECT (figs. 3 and 5B). On this transect two points of similarity to the preceding are apparent. (1) The first and last collections, *Tucker 1467* and *1482*, are fairly representa-

tive *Q. turbinella* and *Q. dumosa*, respectively. (2) All the other collections, *Tucker 1477–1481*, have a higher proportion of intermediates than do the terminal collections. This suggests that the populations from which *Tucker 1477–1481* were collected have been modified through introgression. Even so, in the two populations in which both entities occur (*Tucker 1479* and *1481*), they are separated by evident, although narrow, morphological gaps. The change from populations of *Q. turbinella* to populations of *Q. dumosa* is thus not a gradual merging of one into the other, but a fairly abrupt shift.

As in the preceding transect, the scatter diagrams reveal that in collections that are predominantly *Q. dumosa*, the cup totals are more variable than the leaf and twig totals. In *Tucker 1481*, for example, if we disregard the individuals of *Q. turbinella* and *Q. turbinella*-like intermediates, it is apparent that the others all have leaf and twig totals of 6 or 7 ("good" *Q. dumosa*), while the cup totals extend over the entire range. The collections that are predominantly *Q. turbinella*, however, do not show this difference in variability.

Cajon Pass transect (figs. 4 and 5c). In fig. 4 both terminal collections show a higher proportion of intermediates than corresponding collections on the preceding transects. Nevertheless, *Tucker 1483* represents the "purest" *Q. turbinella* along this transect, being a sample of the first oaks encountered as one ascends from the desert toward Cajon Pass. Here, *Q. turbinella* was growing in association with *Juniperus californica*, *Artemisia tridentata*, and *Yucca* sp. *Tucker 1485*, the only collection of *Q. dumosa*, was isolated from *Q. turbinella* by a gap of several miles along this transect (although they may overlap elsewhere in this general area). At the location of *Tucker 1485*, *Q. dumosa* was growing in association with *Adenostoma fasciculatum*, *Ceanothus crassifolius*, and *Quercus Wislizenii*.

It is obvious that the intermediate part of the range is completely bridged in all three histograms. The greater intermediacy of these collections as compared with those of the preceding transects strongly suggests that introgression has effected a greater merging of *Q. turbinella* and *Q. dumosa* in this area.

As in the preceding transects, the scatter diagram for the single collection of *Q. dumosa* on this transect (*Tucker 1485*) shows the leaf and twig totals to be much less variable than the cup totals. Once again, this is not the case in the collections that are predominantly *Q. turbinella* (*Tucker 1483* and

Explanation of Fig. 5.

Fig. 5. Scatter diagrams of the three transect area populations showing total scores on cup characters (plotted as ordinates) and total scores on leaf and twig characters as the abscissae). Individuals with a preponderance of *Q. turbinella* characters fall to the lower left and those with a preponderance of *Q. dumosa* to the upper right.

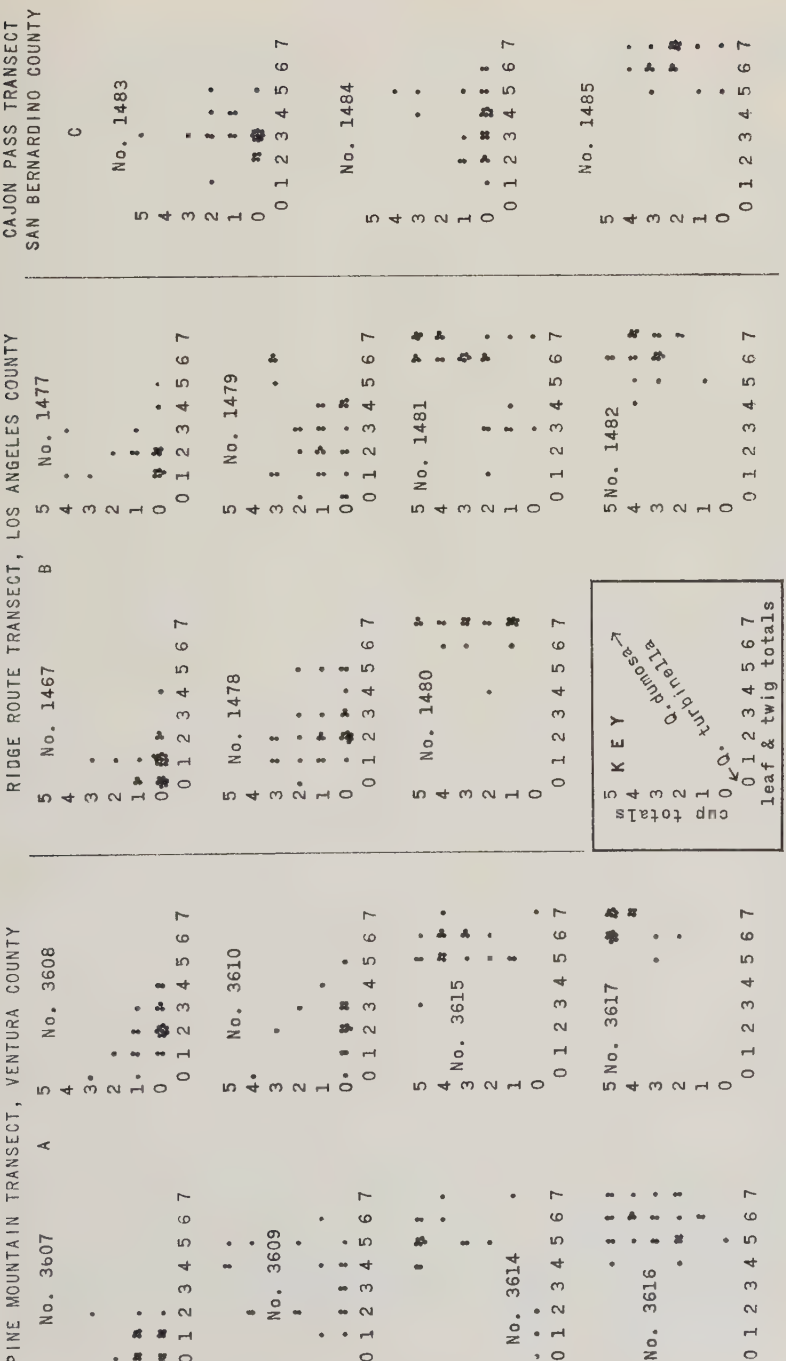


FIG. 5. Scatter diagrams of the three transect area populations

1484). In the latter, cup totals are not conspicuously more variable than leaf and twig totals.

As a tentative explanation of the preceding observations it may be suggested that in the habitats in which *Q. dumosa* predominates, its glossy, green leaves (and perhaps the other leaf and twig characters, also—or genetically linked physiological characteristics) may have a higher selective value than the corresponding characters of *Q. turbinella*. Glossy, green foliage is rather frequent in species of the chaparral formation in which *Q. dumosa* occurs, *Prunus ilicifolia*, *Rhamnus crocea*, and *Ceanothus sorediatus* being common examples. Foliage of this aspect is rather infrequent in desert-border habitats, whereas pale grayish foliage (which, indeed, characterizes *Q. turbinella*) is much more common. It should be borne in mind that selection would exert its earliest effects during the critical establishment stage—the first year or two in the life of a young seedling. Selection at this time would act upon foliage characters, not fruit characters. The latter, obviously, would not be manifested until some years later. If genetic linkage between factors for the cup characters studied and those for the foliage characters studied were only slight (as seems to be the case), then a wide variety of cup characters could become established in a heterozygous population, which, due to rather stringent selection, was much more uniform for foliage characters.

On the other hand, in the more arid habitats where the ranges of these two oaks overlap, one would expect that foliage characters of *Q. turbinella* would have a selective advantage. Be that as it may, the scatter diagrams for such collections as *Tucker 1478* and *1479* (fig. 5B), indicate that *Q. dumosa* genes for both foliage and cup characters have become established in these populations. *Quercus turbinella* genes, conversely, have modified populations of *Q. dumosa* for the most part only in cup characters. In areas where reciprocal introgression has occurred, therefore, the flow of *Q. dumosa* genes into the *Q. turbinella population* has been more pronounced than the reverse.

Although the author has not had the opportunity to study *Q. turbinella* in the field farther south than Cajon Pass, a number of herbarium specimens have been seen from elsewhere in San Bernardino County, and from Riverside and San Diego counties. Just as on the desert slopes north of Cajon Pass, collections from the north slope of the San Bernardino Mountains, though more like *Q. turbinella*, usually show some suggestion of *Q. dumosa*. Eastward and southeastward from the San Bernardino Mountains, characters of *Q. dumosa* are even more prevalent. Although one specimen of fairly characteristic *Q. turninella* has been seen from Morongo Pass (*Epling* and *Robison*, June 24, 1933, LA), most collections from this area

and from the Little San Bernardino Mountains to the southeast exhibit mixtures of the characters of both, and some are nearer to *Q. dumosa.*

The few specimens seen from the Cottonwood and Eagle mountains of Riverside County, although they also contain mixtures of characters of the two, are in general nearer to *Q. dumosa.* These are: Cottonwood Mts., Colorado Desert, *Jaeger,* June, 1921 (UC); north slope of Eagle Mountains, Riverside County, *Alexander* and *Kellogg 2210* (UC); Monsen Canyon, Eagle Mountains, *Alexander* and *Kellogg 2243,* (UC); Palm Canyon, Eagle Mts., *Jaeger,* Dec. 20, 1927 (POM). The single specimen seen from the Santa Rosa Mountains (road from Deep Canyon to Vandeventer Flat, *Munz 12845* (POM), and most of the material from desert-border mountains of San Diego County exhibit a preponderance of *Q. dumosa* characters. An occasional specimen may have paler leaves than usual, e.g. Boulder Park, four miles east of Jacumba, *Dixon 341* (JMT), or thin, only slightly tuberculate cups: Boulder Park, Imperial County, *Gander 4662* (SD). Nevertheless, even those specimens most similar to *Q. turbinella* are distinctly intermediate in the aggregate of their characters. Judging by specimens of *Q. dumosa* from central and western San Diego County, it seems probable that there is complete intergradation with the desert-border forms. In the author's opinion, the material from desert-border mountains of Riverside and San Diego counties is best referred to *Q. dumosa* rather than to *Q. turbinella* (as such specimens have frequently been determined). This pattern of morphological variation suggests that *Q. dumosa* is "swamping out" *Q. turbinella* in these areas. More intensive study is required, however, before this matter can be settled.

Conclusions

1. In the areas of the three transects sampled, *Q. dumosa* and *Q. turbinella* have both become modified through interbreeding (introgression).

2. Along the Pine Mountain and Ridge Route transects, despite the introgression, the species still tend to retain their respective morphological identities.

3. In general, greater modification has taken place in both *Q. dumosa* and *Q. turbinella* along the Cajon Pass transect than along the other transects.

4. Eastward and southeastward from the area of Cajon Pass, *Q. dumosa* characters tend more and more to predominate (judging by miscellaneous herbarium specimens). Indeed, most collections from desert-border mountains of Riverside and San Diego counties are, in general, more similar to *Q. dumosa* than to *Q. turbinella.*

University of California, Davis.
Department of Botany,

LITERATURE CITED

ANDERSON, E. 1936. Hybridization in American tradescantias. Ann. Mo. Bot. Gard. 23: 511–525.

——— 1941. The technique and use of mass collections in plant taxonomy. Ann. Mo. Bot. Gard. 28: 287–292.

GOODWIN, R. H. 1837. The cyto-genetics of two species of Solidago and its bearing on their polymorphy in nature. Amer. Jour. Bot. 24: 425–432.

HEISER, C. B., JR. 1947. Hybridization between the sunflower species Helianthus annuus and H. petiolaris. Evolution 1: 249–262.

STEBBINS, G. L., JR., E. B. MATZKE, and C. EPLING. 1947. Hybridization in a population of Quercus marilandica and Quercus ilicifolia. Evolution 1: 79–88.

TUCKER, J. M. 1952. Taxonomic interrelationships in the Quercus dumosa complex. Madroño 11: 234–251.

A CORRECTION IN THE STATUS OF VIOLA MACLOSKEYI

MILO S. BAKER

In the January, 1953, issue of Madroño I proposed uniting the two white violets known as *Viola pallens* (Banks ex DC.) Brainerd and *V. Macloskeyi* Lloyd and made two combinations under *V. pallens*, which, because of the rule of priority, are not valid. To comply with this rule, it is necessary, much to my regret, to abandon the name *pallens*, so much older in the varietal category, in favor of the earlier specific name *V. Macloskeyi* Lloyd, since the latter has ten years priority over *V. pallens* (Banks ex DC.) Brainerd. Hence, for all material of this species from California and Oregon, known at this time, I propose the name of *V. Macloskeyi* subsp. *Macloskeyi*, and for the northern and eastern material, the name *V. Macloskeyi* subsp. *pallens*. Formal citation for this transferal follows:

VIOLA MACLOSKEYI Lloyd subsp. **Macloskeyi.** *V. Macloskeyi* Lloyd, Erythea 3: 74. 1895. *V. blanda* var. *Macloskeyi* Jepson, Man. Fl. Pl. Calif. 648. 1925. *V. pallens* (Banks ex DC.) Brainerd subsp. *Macloskeyi* Baker, Madroño 12: 18. 1953.

VIOLA MACLOSKEYI Lloyd subsp. **pallens** (Banks ex DC.) comb. nov. *V. rotundifolia* var. *pallens* Banks ex DC. Prodr. 1: 295. 1824. *V. pallens* Brainerd, Rhodora 7: 247. 1905. *V. pallens* (Banks ex DC.) Brainerd subsp. *pallens*, Madroño 12: 17. 1953.

Santa Rosa Junior College,
Santa Rosa, California

REVIEWS

Pollen Morphology and Plant Taxonomy. Angiosperms (An Introduction to Palynology.) By G. Erdtman. xii + 539 pages, 1 plate and 251 figures. 1952. Waltham, Massachusetts: The Chronica Botanica Company; San Francisco: J. W. Stacey, Inc. $14.00.

This work, originating in the Palynological Laboratory in Stockholm, is a resumé of the structure of angiosperm pollen presented from a systematic point of view notwithstanding the fact that the plant families are arranged strictly alphabetically. The book is dedicated to I. W. Bailey, C. Skottsberg, and R. P. Wodehouse. In the foreword Professor H. Humbert of the National Museum of Natural History, Paris, reviews the subject and calls attention to its role as an introduction to palynology and to the ramifications and significance of palynology in science and industry.

In the preface the author points out that his aim is to present the basic principles of palynology as they apply to the main features of angiosperm pollen morphology, and not to present a comprehensive picture of pollen morphology. Your reviewer finds it difficult to discriminate between these subjects as presented in this work. Palynology, we learn, is a term coined by Hyde and Williams for that aspect of spore and pollen science dealing with the structure and markings of the wall, and is not concerned with the cytological interior. As we get into the subject we wonder if this does not make an artificial framework for the science of palynology, which appears to be bound together solely by the common uses, both scientific and practical, to which the characters of the durable spore and pollen coats can be put. The unity of palynology thus revolves around the use of the material rather than its character. This is analagous to the unity of palaeontology as standing apart from biology. The use to which fossils are put in interpretation, both geological and biological, and in science as well as industry, contributes a sense of unity however artificial, and adequately justifies the subject. But just as the biologist may regard the palaeontology of his group as an integral part of biology, so may the pollen morphologist insist that the palynology of pollen is an integral part of pollen morphology.

After a detailed discussion of the techniques developed for the study of palynology, the author goes into an intensive discussion of pollen and spore morphology. One is amazed at the compounding of the terminology that has engulfed such a tiny structure as the wall of a pollen grain or spore. Many terms are explained in the text, and at the end of the work there is a glossary of over 200 entries, many of which contain synonyms not separately treated. The feeling is gained that what the pollen grain lacks in size and structure is compensated for by the compounding of its terminology. Much of this is no doubt necessary and very useful, but I would like to reflect for a moment upon the problems raised.

It has been said that if we understood one another's language there would be little excuse for misunderstanding. There is in this idea an important lesson for those who would elaborate terminology. Special terminology can easily become the Biblical Tower of Babel that confounds understanding. Admitting that Latin is the language of scholars, and that language, within the framework of its rules, is a system of logic for the presentation of ideas, it would seem that the most effective presentation of any subject would lie in a language whose organization and terminology followed rules. To depart from this via the language of the specialist is to embark upon an empirical course which knows neither formalism nor rules, but becomes a lingo of convenience growing independently anew with each burst of

enthusiasm and understandable only to the chosen few. The scholar for instance, can find no linguistic formula for the understanding or interpretation of such words as sexine and nexine as compounded by the palynologist to convey his special meaning. Unless a glossary accompanies each work, the reader is forced to trace such terms back through the special literature until such time as these words find their way into a dictionary. Instead of compounding the linguistic roots of a noun and its modifying adjective, there are added, as prefixes to the word "exine," the letter "s" derived from the adjective "sculptured" and the letter "n" derived from the adjective "nonsculptured." Each prefix is supposed to impart the meaning of the adjective from which it was detached. This is not language! This is jargon! In a science as young as palynology it would pay even now to go back and reconstruct its terminology to make it linguistically understandable and give it the dignity of the language of scholars.

The main body of the work, however, is on a sound foundation and represents a significant contribution to scientific knowledge. In his presentation of a comparative resumé of the pollen characters of each family it is evident that the author is keenly aware of the taxonomic problems of an amazing number of plant families. In family after family the information presented delineates the existing problem in a manner that makes it clear whether or not palynology has anything to contribute toward the solution of the problem. As might be expected, it has much to contribute to some problems and nothing to others. Nevertheless palynology is an aspect of systematic botany that cannot be neglected. Through the techniques developed by Dr. Erdtman and other palynologists, the taxonomist is provided with a new set of comparable facts to employ in the synthesis of relationships.

To assess the usefulness of the work your reviewer sought to determine if the subject as presented made a contribution to several taxonomic problems of which he was aware. He was extremely gratified to find that it either provided additional concomitant characters to bolster ideas that lead one to differentiate groups, or it indicated that my previous doubts were supported by inconclusive evidence from palynology. In some cases evidence tended to refute ideas from other sources. This of course may work both ways in an argument. However we are only interested in the facts, and each interpreter may utilize them toward his objective as he may see fit. In the problems your reviewer chose to investigate, his own views were either satisfied or frustrated by the palynological evidence presented. The main point is that he found something that applied to each problem one way or the other.

In most families the discussion centers around the taxonomic subdivisions whereby genera are aggregated within the families. In addition, very often there is mention of evidence of relationship to other families, and similarities are often pointed out that stimulate questions. In some cases their resemblances seem possibly to have resulted from some aspect of parallel development.

The typography and the binding are excellent examples of the printers' art. In this epoch of expanding concepts of taxonomy, Dr. Erdtman's book will play a very important role by pointing the way to arrive at a host of new comparable facts about plants.—Herbert L. Mason, Department of Botany, University of California, Berkeley.

The Fern Genus Diellia: its Structure, Affinities and Taxonomy. By Warren H. Wagner Jr. Univ. Calif. Publ. Bot. 26: 1–212. 1952. Plates 1–21. 31 figures in text. University of California Press, Berkeley. $3.00.

Diellia is an endemic genus of Hawaiian ferns. Wagner recognizes five species, of which one, *D. unisora* (p. 160), is described as new.

Considering the size and limited range of the genus, *Diellia* has received a remarkable amount of study. Most authors have treated it as a relative of *Lindsaea*. A minority have regarded it as Davallioid. A small minority have recognized it as Aspleniid.

As a naval air navigator, Wagner had many opportunities to collect in Hawaii. After choosing *Diellia* as the subject of his doctor's thesis, he spent two seasons in the field, visiting every known area of collection. He made transplants from the field to California, and many cultures from spores. He also secured for study almost all past collections, including types.

He then compared *Diellia* (all species) with numerous representatives of the three families to which *Diellia* has been ascribed. This study included habitat, complete life-histories, and complete morphology, including prothallia and sporophytes. The chromosome number is $2n = 72$, known to characterize *Asplenium*. His conclusion is that resemblances to *Lindsaea* are superficial or accidental results of convergent evolution. The resemblances to *Davallia* are inconsequential. All valid evidence shows affinity to *Asplenium*. More definitely, the affinity is to the "rock aspleniums," typified by *A. Trichomanes* and including *Ceterach* and *Camptosorus*.

In the reviewer's prejudiced judgment, this is the model generic monograph, the kind foreshadowed by Milde's "Equisetum," in which the taxonomic element is the conclusion, but not the body of the work.

An interesting detail of the conclusion is that the ornate "species," *D. Alexandri*, found on three islands, has evolved independently on each island from *D. erecta*. Being triphyletic, it is not a taxon of any rank, even a variety, but merely a "forma." E. B. COPELAND, Department of Botany, University of California, Berkeley.

Flora of West Virginia. (Part I). By P. D. STRAUSBAUGH and EARL L. CORE. West Virginia University Bulletin, Series 52. June, 1952. $1.00.

Up-to-date state and local floras are an important supplement to the regional floras or "field manuals" now in use in their appropriate areas. By treating fewer taxa, such state or local floras are easier for beginning students to use, especially if the descriptive material for each taxon is accompanied by a good illustration. By treating these taxa more completely—both taxonomically and bibliographically—these smaller floras offer distinct advantages to the specialist or to the more advanced student of botany. Unfortunately, there are only a few such illustrated state floras, and these are usually quite expensive—well beyond the financial reach of most individual botanists and even beyond that of many of the less heavily endowed schools. Needless to say, this sharply limits their potential usefulness.

With this in mind it was a very pleasant surprise to find, on reviewing this well-illustrated first volume of the Flora of West Virginia issued as a bulletin of the University of West Virginia, that it cost only one dollar. The authors intend two or three additional fascicles to complete the series. If these later fascicles sell for the same amount as the first, the entire illustrated set, treating "approximately 2,000 species," will be available for less than five dollars.

Part I of the series treats the Pteridophyta, the gymnosperms, and the monocotyledons growing without cultivation in West Virginia. The dichotomous keys to the genera and species appear well done, but the lack of a key to the families may handicap some students. The lack of an index in each volume will, at times, be a handicap to beginner and specialist alike, especially in reference to common names. Following the style of Fernald's recent edition of Gray's Manual, the meanings of all generic and specific names are included

as part of the treatment of these taxa. The illustrations appear to depict accurately the diagnostic morphological criteria of each series, and the drawings—usually opposite the descriptive material of a given species—are relatively large and are not crowded on the plates. These illustrations have come from several sources and are therefore not always uniform as to style of labeling. This esthetic consideration, however, in no way detracts from their scientific accuracy or usefulness. The heavy paper cover is quite attractive and would suffice unless the book got extended use as a field manual. Even so, the volumes could be rebound and still cost much less than other floras of this type. It is hoped that this series will start a trend to take such illustrated floras out of the class of "collectors items" and put them in the hands of the interested people who need them. C. RITCHIE BELL, Botany Department, University of California, Berkeley.

Downs and Dunes, Their Plant Life and Its Environment. By SIR EDWARD SALISBURY. xiv + 328 pp., 100 figs., 32 plates. 1952. G. Bell and Sons, Ltd., London. 45 s. net.

"Downs and Dunes" is an elaborately detailed account of the vegetation of the chalk downs, limestones, and sand dunes of Great Britain. Floristics and ecology are included as well as some of the dynamics of plant geography. The book is written in a very readable style, here discussing the situation in nature solely from observational evidence and there discussing a fact documented by experiment, thus reflecting an enormous amount of careful observation and investigation. It is copiously illustrated with beautiful photographs and line drawings. In all, down to the abundant ecological notes on individual species, it is a very informative work.

Although nowhere does the author so state them, conclusions as to geographic affinity seem to assume an overworked concept of unity in floristic origins that does not emphasize any coincidence in ecological requirements. One fails to grasp any other meaning or purpose to such items as geographic elements ("Mediterranean element") or components ("oceanic component").

Since the words "downs" and "dunes" come from exactly the same etymological root, the American reader not at home with the word "down" would have liked to have had a clearer presentation of the geographical or ecological connotation of "downs versus dunes." One pieces tgether that the downs are on chalk that is almost pure calcium carbonate and the duner are of sand largely of mixed calcereous and siliceous origin. —HERBERT L. MASON, Department of Botany, University of California, Berkeley.